

Parasitism and the Movements of Intertidal Gastropod Individuals

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Abstract. Movements of marked individuals of *Ilyanassa obsoleta* (n = 500) were charted in an intertidal environment for about one week. At the end of observations, 260 marked individuals, which had been sighted 1017 times collectively, were recaptured and examined for trematode infections. Six trematode species were found in 19 infection combinations including uninfected, singly, doubly, and triply infected snails. We know that most snails found high on beaches and on sandbars carry *Gynaecotyla adunca* infections. It has been hypothesized that this host behavior modification is a parasite adaptation to enhance cercarial transmission to a semi-terrestrial next host. Observations reported here support this hypothesis and reveal some of the complexity in the behavior imposed on *I. obsoleta* by *G. adunca*. Individuals that were uninfected or infected with other parasites demonstrated no unique movement patterns, but individuals infected with *G. adunca* made repeated excursions into the upper shore habitat. These excursions were timed so that host-parasites were left emerged at high elevations primarily during nighttime low tides. Because many snails were multiply infected, data presented support the idea that gastropod populations have the potential to be used as systems for the study of the nature of ecological and evolutionary interactions among parasite species.

Introduction

Spatial and temporal patterns associated with intertidal animals have been studied by many authors. A recent review (Foster *et al.*, 1988) discusses the ecological

factors thought to cause these patterns. However, pointing to a shortage of specific studies, these authors expressly (p. 13) did not include the effects of parasitism in their discussion, although they noted that the effects of parasites on their hosts can be substantial. Several studies have examined the movements of intertidal gastropods (*e.g.*, Underwood, 1977; Borowsky, 1979; Hazlett, 1984), but parasitism has not often been considered an important factor in these studies. Gastropods are an important component of marine and estuarine benthic systems. That parasites should not be ignored in these systems has been shown by previous studies with the mud snail *Ilyanassa obsoleta* and its trematode parasites (Sindermann, 1960; Stambaugh and McDermott, 1969; Curtis and Hurd, 1983; Curtis, 1985, 1987). The significance of parasitism has also been shown for at least one other abundant gastropod, *Littorina littorea* (*e.g.*, Sindermann and Farrin, 1962; Lambert and Farley, 1968; Williams and Ellis, 1975).

In a previous observation (Curtis, 1987) I noted a relationship between trematode parasitism and vertical zonation of the mud snail *Ilyanassa obsoleta* on the shore. Snails found high on beaches and on sandbars were usually parasitized by *Gynaecotyla adunca*. Snails unparasitized or parasitized with other species remained at lower levels. Data were interpreted to mean that the parasite alters the normal behavior of the host snail to enhance transmission of cercariae to semi-terrestrial (beach-dwelling) crustacean second hosts. Many parasites alter host behavior to enhance host-to-host transmission by means of predation [see Dobson (1987) for references], but this is apparently the first observation suggesting altered behavior with the adaptive advantage of enhancing cercarial transmission.

Thus far, inferences concerning the behavior-altering

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capacity of *Gynaecotyla adunca* have been drawn from correlative population-level data with no attempt to determine the behavior of individual snails. Observations of individual host behavior are necessary because one cannot determine the exact composition of the altered behavior by comparing parasitism in populations at different vertical levels on the shore (Curtis, 1987). Many questions are left unanswered by this approach. Does the same host repeatedly move onto the same area of beach or sandbar? If repeated visits occur, is there a schedule? Do hosts always move to a similar vertical position? Does this mean that *G. adunca*-infected snails move around in the habitat significantly more than other snails? In general, just how simple or complex is the altered behavior imposed on *Ilyanassa obsoleta* by this parasite?

Data presented in this paper help address these questions. Positional histories of individually marked snails with various infections (including uninfected) were charted in a natural sandflat environment for approximately one week. Data indicate that *Gynaecotyla adunca*-infected snails, despite the presence or absence of co-occurring trematodes, have a complex, patterned behavior that is much different from the behavior of snails when unparasitized or parasitized by other trematodes. In a broader sense, the results illustrate the depth to which parasites become insinuated into ecological systems and their contribution to the complexity of those systems. Additionally, the high frequencies of double and triple infections revealed by this (and other) work support the idea that host gastropod populations could be more useful as systems for the study of parasite species interactions than is currently appreciated.

Materials and Methods

The experiment took place during July 1985 on the Cape Henlopen sandflat in Delaware Bay (described in Curtis and Hurd, 1983). The same sandbar area that had been used in 1984 (Curtis, 1987) was used again. The configuration and position of the sandbar had changed somewhat over the winter, so on 2 July sandbar topography was again mapped (Fig. 1) using the methods described in Curtis (1987). A 3 × 5 m plot was marked out at the peak of the sandbar and a pipe was driven deep into the center of the plot as a vertical (zero elevation) and horizontal reference point for measurements made during the experiment (see Fig. 1).

Cape Henlopen has two low and two high tides per day that are roughly equal in range (ca. 1–1.5 m). The sandbar peak was emerged for approximately 3 h on either side of low tide and submerged for approximately 3 h on either side of high tide.

In 1984 there was a clear correlation between proportion of snails parasitized by *Gynaecotyla adunca* and ele-

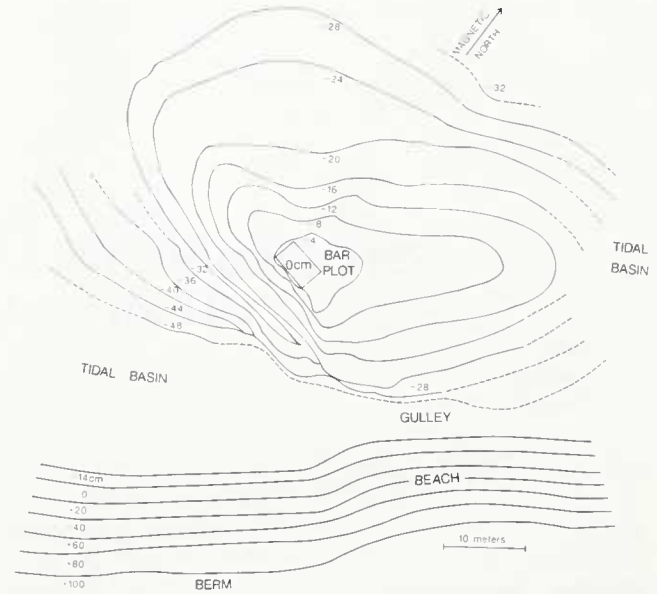


Figure 1. A sketch map of the Cape Henlopen sandbar used for this study. Zones of elevation and position of the 3 × 5 meter plot are shown.

vation. To determine whether this was also true in 1985, snails were collected from the sandbar peak area ($n = 185$) and, for comparison, from 11 sites on the sandflat peripheral to the sandbar ($n = 125$). Sandflat snails were collected from areas at least 28 cm down from the sandbar plot (Fig. 1). These were examined for size, sex, and parasitism as described in Curtis (1985).

Generally, the design of the experiment involved collecting two sets of snails: sandbar/beach snails (which were likely to be infected with *Gynaecotyla adunca*); and sandflat snails (which were unlikely to be so infected). Snails in both sets were marked individually and released on the sandbar. The sandbar, adjacent sandflat, and beach were searched for marked individuals during each subsequent low tide for about one week. As marked individuals were located, their positions relative to plot center were recorded using polar coordinates.

More specifically, snails were marked with numbered insect tags glued onto a dried and roughened shell area with clear fingernail polish. Sandflat snails ($n = 250$) were collected on 15 July during the 1309 h low tide. (All times are Eastern daylight savings time.) They were measured for size, marked, and retained in the laboratory until release. Sandbar/beach snails ($n = 250$) were collected during the 0216 h low tide on 16 July. They were measured, marked, and retained in the laboratory. On the next low tide (16 July, 1354 h) the 500 marked snails were released on the sandbar in 20 groups of 25 (13 sandbar/beach snails plus 12 sandflat snails, or the reverse) placed at equal intervals along a circumference

Table I

Nearby physical conditions and numbers of snails at the sandbar peak (3×5 m plot) during the 16–24 July 1985 Cape Henlopen experiment with individually marked *Ilyanassa obsoleta*

Low tide #	Time EDST	Lighting	Ta	Tw	Sal	Snails in plot	% marked
0	1354	L	25	24	29	(marked snails released)	
1	0257	D	24	23	28	42	12
2	1437	L	27	28	?	4	25
3	0339	D	21	21	?	63	40
4	1522	L	29	32	28	15	27
5	0418	D	18	19	18	102	37
6	1608	L	24	28	29	3	33
7	0500	D	23	21	27	70	36
8	1655	L	28	30	30	7	0
9	0543	D	25	23	24	27	48
10	1745	L	26	26	26	3	67
11	0627	D	24	24	26	45	40
12	1840	L	26	26	29	15	47
13	0713	D	20	21	?	39	36
14	1938	D	23	23	30	14	27
15	0803	L	—	—	—	—	—
16	2040	D	—	—	—	—	—

Abbreviations: Ta and Tw = air and water temperature ($^{\circ}\text{C}$); sal = salinity (g/kg); and lighting conditions (L = light, D = dark). A tide is labeled "dark" if it occurred between sunset minus one hour (1900 h) and sunrise plus two hours (0800 h).

at a 10-m radius from the plot center (Fig. 1). On this and all subsequent low tides during the experiment, all snails inside the plot were evicted (scattered just outside the plot). Thus on any given low tide, counts of plot snails reflected those that had moved in during the previous high water and remained.

The procedure for locating marked snails involved searching the sandbar and its periphery. Whenever a marked snail was sighted, mark number, time, meters from plot center, and number of degrees clockwise from magnetic north were noted. The sandbar and adjacent sandflat were searched in ever wider circles until water became too deep (about 15 cm) to observe snails. Depending on tidal range, the sandbar and adjacent areas could be effectively searched for up to three hours on one low tide. If the release tide is tide zero, searches were performed and snail positions noted through tide 16 (24 July, 2040 h). Most marked snails were recollected on tides 14–16. Many marked snails were recollected after tide 16 (through 28 August). Sightings of these snails during the experimental week were used, but positions recorded at recollection were not.

By transferring position of a snail at sighting to the contour map of the sandbar (Fig. 1) elevation of the snail at that sighting and net distance moved since the previous sighting were determined. Snail elevations were assigned to discrete elevation zones (0, 2, 4, 6...50 cm below plot center). A mean elevation at sighting was calculated for each recovered marked snail. Net distance moved per tide by a snail between sightings was deter-

mined by converting polar coordinates from field measurements to rectangular coordinates, calculating distance between the two points and dividing by the number of elapsed tides. To reduce any effects of the marking and release procedure, movements between points of release and first sightings were excluded. A mean net movement per tide (rounded to the nearest meter) was calculated for each recovered marked snail that was observed at least twice. Recovered snails were examined in the laboratory by dissection so individual snail histories during the experiment could be compared based on parasitism and other characteristics. Comparisons among snails with different infections in terms of elevation on the sandbar and net distance moved were made using nonparametric statistical methods (Sokal and Rohlf, 1981).

Results

Table I shows some of the physical conditions prevailing on low tides during the experiment as well as numbers of snails entering the 3×5 m plot at the sandbar peak during the previous high water. Temperatures and salinities were in the usual ranges for Cape Henlopen. No information is given for tides 15 and 16 because from tide 14 on snails were being collected as sighted. In Table I, tides are classified as occurring under light or dark conditions, and it is apparent that more snails were present in the plot on dark low tides (mean = 50.25, S.D. = 27.53) than on light low tides (mean = 7.83, S.D.

Table II

Statistics for shell size and sex ratio, and number of snails in each trematode infection category, for groups of *Ilyanassa obsoleta* collected and examined in connection with the snail movement experiment

Parameter	Unmarked snail samples		Recollected (marked) snails
	Sandbar peak	Sandflat	
Shell height (mm)			
mean	21.1	20.3	21.4
S.D.	1.7	2.3	1.5
% female:% male	47:53	50:50	44:56
Infection*			
NI	39	69	32
Hq	0	10	8
Ls	0	4	5
Zr	2	35	19
Av	0	2	5
Ga	78	0	106
Dn	0	1	1
HZ	1	1	3
HG	0	0	3
LZ	1	1	4
LG	22	1	31
ZA	1	0	0
ZG	25	0	30
AG	5	0	6
GD	1	0	0
GSt	0	0	1
LZG	5	1	3
LAG	2	0	3
ZAG	1	0	0
TOTALS	185	125	260
% Ga-infected	75.1	1.6	70.4

* Abbreviations: NI = not infected; Hq = *Himasthla quissetensis*; Ls = *Lepocreadium setiferoides*; Zr = *Zoogonus rubellus*; Av = *Austrobilharzia variglandis*; Ga = *Gynaecotyla adunca*; Dn = *Diplostomum nassa*; St = *Stephanostomum tenue*; multiple infections are abbreviated with the generic initials of the species involved (e.g., ZAG = ZrAvGa triple infection).

= 5.74). Table I further shows that on most tides many snails in the plot had marks, which suggests that they made up a substantial proportion of total snails using the sandbar. Table II shows that the groups of snails examined in this study did not differ significantly in terms of age (shell height) or proportions of males and females. However, it is clear that snails visiting the sandbar peak (plot) were largely *Gynaecotyla adunca*-infected, whereas snails from the adjacent sandflat were not (Table II, unmarked snails). Table II also shows the variety of multiple infections present and, in particular, the large proportion of *G. adunca* infections that were combined with other trematode infections: of the 324 observed *G. adunca*-infected snails in Table II, nearly half (43.2%) were multiply infected.

Of the 500 snails marked and released, 260 were ultimately recovered. Frequencies of trematode infections among recollected marked snails, which were sighted 1017 times collectively over the 16 tides, are shown in Table II. Based on initial collection site, there were two groups of marked snails: a sandbar/beach group (n = 250, mean shell height = 21.5 mm, S.D. = 1.5); and a sandflat group (n = 250, mean shell height = 20.8 mm, S.D. = 1.5). The likelihood of sighting and recovering a snail was clearly different for individuals in the two groups: 74.6% of the sandbar/beach snails were recovered (93.6% were sighted at least once after release); only 31.2% of the sandflat snails were recovered (68.4% were sighted after release). Almost all (99.5%) recovered snails from the sandbar/beach group (n = 182) had *Gynaecotyla adunca* infections, while very few (2.6%) recovered snails from the sandflat group (n = 78) had this parasite. Marked snails apparently stayed near the sandbar during the experiment because regular searches of the adjacent beach (Fig. 1) and a neighboring sandbar 30 m SW revealed no marked snails. The less frequent observation and greater loss of marked sandflat group snails can be explained by their being dispersed in a larger area (see below).

Three marked snails were sighted in the area of the 1985 sandbar during July and August 1986. By this time, the experimental sandbar no longer existed. Snail A was uninfected when examined and had a shell height of 20.0 mm (19.9 mm when marked). It was observed twice in 1985 around the periphery of the sandbar. Snails B and C were both double infected with *Zoogonus rubellus* and *Gynaecotyla adunca* and had shell heights of 24.9 and 23.8 mm (24.7 and 23.7 mm, respectively, when marked). Both snails had been sighted several times (total = 8) on the peak of the sandbar in 1985. Such data are subject to multiple interpretations, but indications are: (1) that growth for these large snails was slight during the previous year; and (2) based on behavior, snail A was probably not infected in 1985 and remained so, while snails B and C were both infected with (at least) *G. adunca* in 1985 and had carried their infections through the winter.

Sightings of marked snails during the experiment provided information on elevation at sighting and movement between sightings for individuals with various single and multiple trematode infections. Because *Gynaecotyla adunca*-infected snails aggregated near the sandbar peak, probability of observing these snails was enhanced. Snails that did not behave this way were dispersed in a larger area (the outer edge and periphery of the sandbar), and the probability of observing them was reduced. Activities of *G. adunca*-infected snails would be over-represented in the data if all the individual sightings (range = 1-9/snail) were used as datum points. To correct for

Table III

Relationship between trematode parasitism and elevation at sighting (cm down from bar peak) of marked *Ilyanassa obsoleta* individuals on a Cape Henlopen sandbar*

Parameter	Parasitism								
	NI	Hq	Ls	Zr	Av	Ga	LG	ZG	AG
# marked snails	32	8	5	19	5	106	31	30	6
Total # sightings	78	17	18	53	14	460	151	115	34
Median of mean elevs. (cm)	38	34.7	30	38.7	42	5.5	4.7	4.5	4.5
Range (cm)	3-50	33-48	22-47	25-50	34-51	0-32	0-19	0-30	1-8
Avg. rank	201	205	195	209	219	93	75	88	79

* There was a significant effect of parasitism on the mean elevations of individual snails (Kruskal-Wallis test, $H = 139.456$, d.o.f. = 8, $P < 0.001$). Higher average ranks denote lower elevations. Abbreviations as in Table II.

this, I used mean elevation at sighting and mean net movement per tide between sightings as datum points for each snail. This procedure emphasizes infrequently sighted snails (*i.e.*, not *G. adunca*-infected). Neither tendency is desirable, but using the mean value for each snail leads to more conservative comparisons because statistical tests are not swamped with the behavior of frequently observed *G. adunca*-infected snails.

Categories of infection with fewer than five snails were eliminated from Tables III and IV. Table III shows that the elevation of *Ilyanassa obsoleta* at sighting was influenced by parasitism. Individuals infected with *Gynaecotyla adunca*, either singly or in multiple, were sighted at higher elevations on the sandbar (lower average ranks in the table) than uninfected or otherwise infected individuals. Table IV shows that net movement per tide of individual snails was also influenced by parasitism. It should be recognized that these measurements record minimum movement. Snails could not have moved less than the distances measured, but undoubtedly moved more. Average ranks and medians (Table IV) show that there were

two groups of snails with respect to net movement per tide; those infected with *G. adunca* and those not. A statistical comparison of just these two groups confirms that *G. adunca*-infected snails moved around more than other snails (Mann-Whitney U Test, $U = 5657.5$, $P < 0.001$).

A long interval between pairs of sightings could affect the magnitude of calculated net movement per tide. With snails remaining in the same general area, as many did in this study, this would probably lead to an underestimation of net movement. If time between sightings was routinely greater for snails lacking *Gynaecotyla adunca* (which were seen less often) compared to those infected, this could introduce a bias and compromise the result (Table IV) that snails with *G. adunca* moved around more than other snails. The range of elapsed tides between sighting pairs was the same for both groups (1-13). The mean number of tides between pairs of sightings for all recollected *G. adunca*-infected snails (Table II) was 2.5, with 91% of sighting pairs ($n = 625$) coming four or fewer tides apart; the corresponding mean for recollected

Table IV

Relationship between trematode parasitism and mean net movement between pairs of low tides for individually marked *Ilyanassa obsoleta* on a Cape Henlopen sandbar*

Parameter	Parasitism								
	NI	Hq	Ls	Zr	Ga	LG	ZG	AG	
# marked snails	22	6	5	17	104	30	28	6	
Total # net moves obs.	48	9	13	35	351	120	84	27	
Median of mean net moves (m)	1.6	1.5	1.7	1.8	2.5	2.6	2.9	2.5	
Range (m)	0-15	0-4	1-3	0-7	0-11	0-8	1-8	1-3	
Avg. rank	75	83	67	90	114	121	130	113	

* There was a significant effect of parasitism on net movement per tide of individual snails (Kruskal-Wallis test, $H = 16.987$, d.o.f. = 7, $P < 0.02$). Higher average ranks denote more movement. Abbreviations as in Table II.

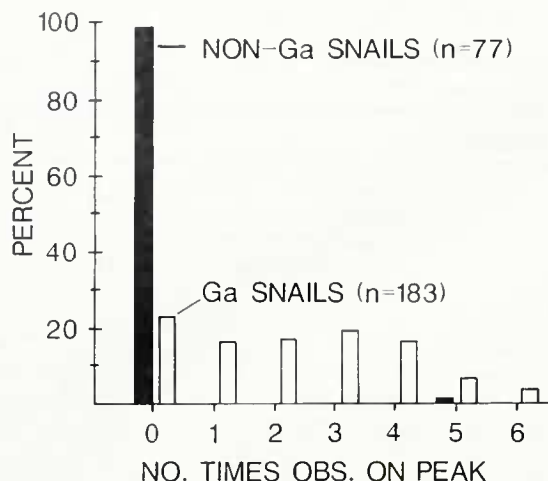


Figure 2. Frequencies of visitation to the sandbar peak (upper vertical 4 cm in Fig. 1) by *Ilyanassa obsoleta* infected with *Gynaecotyla adunca* (Ga snails) and those not infected (non-Ga snails).

snails without *G. adunca* was 3.4, with 75% of sighting pairs ($n = 131$) coming within four tides. Therefore, the usual number of tides between sightings was similar (1–4) for both groups of snails. Even if longer periods between sightings tend to reduce calculated net movements per tide, relatively few measurements would have been involved. Moreover, both groups of data would have been affected similarly. A biased underestimation, on this account, is unlikely.

Frequency of visitation to the sandbar peak by the 260 recovered snails (Table II) is shown in Figure 2. Snails not infected with *Gynaecotyla adunca* almost never showed up in the upper 4 cm area of the sandbar. Only a single snail not infected with *G. adunca* (recorded as uninfected) made multiple visits to the peak. Among *G. adunca*-infected snails, however, many individuals visited the peak several times (up to six) during the 16-tide experiment. Visitations could have been more frequent and regular than indicated (Fig. 2) if buried marked snails escaped notice on some tides. In any case, it is clear that many host snails made repeated excursions onto the same sandbar peak.

The behavior of *Gynaecotyla adunca*-infected snails has a diurnal component because they are most frequent on beaches and sandbars during night low tides (Curtis, 1987; Table I). The diurnal pattern of visitation to the sandbar peak by host individuals, which results in this observation, is revealed by the following data. The peak is defined here as the area within the 4-cm contour (Fig. 1). Among *G. adunca*-infected snails, 112 were observed on the peak two or more times. Most sightings for these (90%, $n = 377$) were on night low tides. None of these snails was sighted exclusively on daytime low tides; 72% were sighted exclusively on nighttime low tides and 28%

showed up on both day and night low tides. Among the 28% seen on both dark and light tides, 71% of sightings were on dark tides. Therefore, host-parasites were typically emerged during night low tides with daytime emergence being relatively infrequent.

Among recovered *Gynaecotyla adunca*-infected snails, 77 were sighted on both light and dark low tides. Were they sighted at similar elevations on both types of tides? In a Wilcoxon Signed-Ranks Test for two groups (paired observations), these snails had a significantly higher elevation when sighted on the sandbar at night (mean = 7.0 cm down from peak, range = 0–34) than when sighted during the day (mean = 9.5 cm, range = 0–50) (Wilcoxon $T = 869.5$, $P < 0.002$). Therefore, not only did infected snails tend to make night visits to the sandbar, but on those night visits they positioned themselves higher than on day visits.

Discussion

My results show that *Ilyanassa obsoleta* infected with *Gynaecotyla adunca* exhibits a complex behavior unlike that of snails lacking this parasite. These snails make repeated migrations (Fig. 2) to the higher reaches (Table III; Curtis, 1987) of sandbars and beaches, and these excursions entail a generally greater amount of movement per tide than that demonstrated by other snails (Table IV). These migrations leave hosts emerged primarily (but not exclusively) during low tides that occur at night (Table I). When a host snail is sighted on both night and day low tides, it is usually found at higher elevations at night.

All this suggests that there is adaptive value to the parasite in repeatedly inducing its host to be located high on the shore during nighttime low tides. *Ilyanassa obsoleta* is the main first intermediate host for *Gynaecotyla adunca*. Definitive hosts include any of a variety of shore birds and certain fish (Hunter, 1952) and mammal species (Harkema and Miller, 1962). I proposed previously (Curtis, 1987) that the adaptive value lies in an enhanced probability of cercarial transmission to semi-terrestrial, crustacean second intermediate hosts [the amphipod beach-hoppers, *Talorchestia longicornis* (Rankin, 1940) and *T. megalophthalmia* (Hunter and Vernberg, 1957) or the fiddler crab *Uca pugilator* (Hunter, 1952)]. The present results support, and allow refinement of this general hypothesis.

Fiddler crabs do not inhabit Cape Henlopen, but beach-hoppers do. It should be noted, however, that these second hosts are beach (not sandbar) dwellers. Because the basic behavior of infected snails is the same on sandbars and beaches (Curtis, 1987), the two habitats are apparently indistinguishable by infected individuals. It is worth noting that, in adaptive terms, migrating up and down Cape Henlopen sandbars appears to be a waste of

parasite time and energy because the next host is not found there. Presumably, however, over the geographical range of the parasite, a next host is present often enough that parasite fitness is enhanced by inducing host vertical migrations regardless of whether a second host is present or absent on a particular shore.

What cues could be used to control the migration? Based on field observations (Curtis, 1987), I concluded that the day-night difference in numbers of host-parasites on the sandbar is a matter of differential immigration during submergence, not differential emigration during emergence. Thus, when a sandbar or beach is examined at low tide, snails found there had moved into position hours before during the previous high tide. This means that the host-parasite tends not to move up the shore during a high tide to be followed by a daytime low tide, but tends to do so on a high tide that will be followed by a nighttime low tide (Curtis, 1987; present results). Therefore, a remarkable feature of the host-parasite is its ability to track and respond to high tides associated with appropriate future low tides.

From an adaptive standpoint, why avoid stranding the host on daytime low tides? Curtis (1987) noted that the diurnal difference in migratory behavior could be adaptive because (1) it matches diurnal behavior patterns of the next host or (2) it lessens the risk of desiccation to the host or the parasite. Beach-hoppers (Talitridae) tend to be active at night and burrow during the day (Kaestner, 1970; pers. obs.), making (1) above very probable. In this study, individuals infected with *Gynaecotyla adunca* were observed on daytime tides and later again on nighttime tides, which shows that daytime exposure is not lethal to the infection. Anyway, parasite stages within the host are probably not the ones at risk. More likely, cercariae cannot survive the rigors of exposure outside the host during daytime tides. Tentatively then, host excursions onto a daytime beach would reduce the parasite's fitness for two reasons: the next host would not be around to infect; and released cercariae would not survive until hosts become active on a subsequent nighttime tide.

In studies where the effect of trematode parasitism on intertidal snail movement has been considered (Sindermann, 1960; Lambert and Farley, 1968; Stambaugh and McDermott, 1969; Williams and Ellis, 1975), the general conclusion has been that parasitism inhibits movement of the host. Perhaps parasitism does decrease gastropod movement in some circumstances, but in this study (Table IV) it only increased it. Snails infected with *Gynaecotyla adunca*, singly or in combination with other species, could be distinguished from the rest because, consistent with their migratory behavior, they exhibited greater mean net movement per tide. However, uninfected snails could not be distinguished from infected ones (ex-

cept *G. adunca*-infected) based on movement. This result suggests that, during summer and in terms of locomotion in the field, *Ilyanassa obsoleta* is not significantly impaired by trematode parasites.

Gynaecotyla adunca is found in many multiple infections (Curtis, 1985, 1987, Table II) and has an overriding influence on the host regardless of the presence or absence of other trematodes (Fig. 2, Tables III, IV). This suggests that interactions with other trematode species are likely. Most accounts of ecological and evolutionary relationships among co-occurring helminths emphasize the interactions of adult parasites in vertebrates (e.g., Price, 1980; Holmes, 1983, 1986; Holmes and Price, 1986). Holmes and Price (1986) and Holmes (1986) delineate three hierarchical levels of parasite assemblage organization: infra-, component, and compound communities. Data from this study (Table II) are, in themselves, probably too few for meaningful analysis, but in kind they stand to reveal organization at infra- and component levels.

The development of more host-parasite systems amenable to study is essential to progress in the field of parasite community (guild) ecology (Price, 1986). Larval trematodes in marine gastropods have not been much studied in this context because multiple infections are, or are considered to be, too infrequent (e.g., see Vernberg *et al.*, 1969). Gastropod-trematode systems have been analyzed for parasite species interactions (see Rohde, 1981 and references therein) and co-occurrence interactions have been noted, but such systems have probably been underutilized. Field studies (Cort *et al.*, 1937; Rohde, 1981; Curtis, 1985, 1987) show that multiple infections can be commonplace. In this study, 570 snails were examined (Table II): 75.4% were infected (19 different combinations); 26.7% were multiply infected. *Ilyanassa obsoleta* individuals and populations should be added to the list of systems in which interactions among parasites can be studied.

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